COMPARATIVE STUDIES ON THE EXTERNAL ACOUSTIC MEATUS

I. THE MORPHOLOGY OF THE EXTERNAL EAR OF THE ECHIDNA (TACHYGLOSSUS ACULEATUS)

RICHARD TUCKER
Veterinary School, University of Queensland, Brisbane, Australia

(Plates iv-v)

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Synopsis

The study of the external ear of *Tachyglossus aculeatus* revealed that echidna has an intramuscular pinna which merges with the external acoustic meatus. The latter, a completely extracranial structure, consists of four chambers, each marked off by a sharp bend in the meatus. The morphological and functional significance of this arrangement is discussed.

INTRODUCTION

The marked specialization of the external ear of echidna (*Tachyglossus aculeatus*), combined with the conspicuous taxonomical position of the monotremes, makes the study of the acoustic passages of the echidna interesting, useful, and convenient as a starting point for broader investigations on the comparative histology of the external acoustic meatus.

The comparative histology of the external acoustic meatus is at present a virgin field. Concentration on the ear of the human and the dog prompted by clinical interests left us without morphological perspectives and without the basis for assessment of adaptations which can only be understood through comparative investigations. With this in mind, a variety of species were studied. The present paper is the first of a series of reports on the external acoustic meatus.

MATERIALS AND METHODS

The external acoustic passages of echidna were investigated by means of anatomical dissections and by study of unsaturated polyester resin casts.

THE MORPHOLOGY OF THE PINNA

The external opening of the acoustic meatus of the echidna is hidden completely by surrounding spines and hairs. Topographically, it is located close to the ventral margin of the region of the coat which bears spines and the distance between the anterior margin of hair and the opening of the external ear equals roughly the distance between the anterior end of the maxilla and the outer margins of the hair (Plate iv, fig. 1). However, the removal of skin makes the large opening leading into the spacious cavity visible (Plate iv, fig. 2). More complete dissection reveals that the cavity is in fact a pinna embedded in the skin and musculature. The pinna is orientated dorso-ventrally with its cartilaginous margin, bending medially to form a roughly triangular hiatus covered with the relatively short and dense hairs (Plate v, fig. 5). In the ventral portion of the pinna the lateral margins of the cartilage merge, forming a large goblet-like structure. The median surface of the pinna is smooth and flat (Plate v, fig. 6). The pinneal cavity passes at once but at a right-angle into the external acoustic meatus.

The External Acoustic Meatus

The diameter of the external acoustic meatus is about a quarter of that of the pinneal cavity. The meatus itself is tortuous: at first (in the para-pinneal portion) it runs anteriorly, then medially and finally turns dorsally to reach the base of the skull (Plate iv, fig. 4, and Plate v, fig. 6). The meatus is narrowest at its cranial end and widest in the proximity of the pinna (Plate v, fig. 7). On the internal surface of its wall the distinct crista is present (Plate iv, fig. 6). The cranial opening of the meatus is elongated (Plate v, fig. 8). The sharp angles between the various portions of the external acoustic passages divide the extracranial acoustic meatus and pinna into four (4) distinct chambers, the most external being formed by the pinna; this is elongated and contains hairs. The second chamber, directed anteriorly, is relatively spacious. The third and fourth are smaller in diameter and develop the internal cartilaginous crista. The wall of the meatus consists of cartilaginous " ribs " connected by a membrane.

Discussion

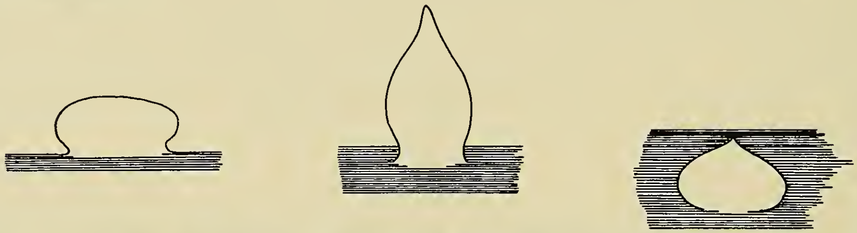
The external ears of all mammals and birds have the same general functions. To these belong: (1) expression; (2) temperature regulation; (3) protection of the middle and inner ear; (4) the isolation and localization of sound; and (5) the transmission of sound. These functions are modified from species to species. Nevertheless, they form a convenient reference frame for discussion and the assessment of adaptations and modifications within the particular auditory passages. Therefore, the conditions described above will be discussed in relation to these functions.

In most mammals the function of expression belongs wholly to the pinna, the muscular plate of the *platysma myoides* and to the facial nerve. The expressive ability of the pinna is governed by its size and the degree of its mobility. Animals of terrestrial habitat such as the horse, ox, and dog have large and freely mobile pinnae. Aquatic animals and those with subterranean or burrowing habits have a pinna of considerably reduced size, while primates of arboreal habit or descent have rather immobile ears. The musculature of the external ear develops from the *platysma myoides*, the cutaneous muscle of the second branchial arch, and the degree of mobility of adult external ears depends on the final connection of the pinna with this muscle. The human ear has lost most of its muscular connections, while the mobile and expressive ear of most terrestrial animals is connected with the platysma by special muscular strands—the auricular muscles. These muscles as well as the platysma are supplied by fibres from the facial nerve so that the expressive movements of the ears are stimulated by fibres from the same area of the central nervous system as those connected with the facial expression in man.

According to McKay (1894), in echidna the *panniculus carnosus* consists of three layers, and is innervated only by the cervical nerves, the auricular region being supplied by the second cervical nerve. However, Westling (1889) describes innervation of subcutaneous cervical muscles by both the facial and cervical nerves. Also Edgeworth (1935) pictures (after Schulman) the platysma in echidna together with *M. sphincter colli superficialis* in the area of the external acoustic meatus.

The intramuscular position of the pinna in echidna changed also the character of its movements: pinna is not moved by the muscle; instead, it is moved with the muscles. It is in fact a muscular cartilaginous insertion (*insertio cartilaginea*) comparable in a sense with the tendinous insertions in the rectus system (Tucker, 1955). This insertion is large and isolated. The existence of different relations of pinna to the musculature (the echidna type being an extreme case) enables us to distinguish between the three types of pinna in mammals.

In relation to the platysma the mammalian pinna can acquire an *extra-platysmal* position, with no, or only negligible, connections with this muscle—e.g. *Homo* ; or a *supra-platysmal* position with only the deep portion of pinna connected with platysma and supplied by strong auricular muscles, e.g. Bovidae, Equidae. In echidna, we have the case of an intramuscular pinna connected with *panniculus carnosus*. The different types of relationship between the pinna and the musculature in mammals are shown diagramatically in Text-fig. 1. There is probably a relative lack of expression in echidna due to the factors mentioned above.



Text-fig. 1. Diagram showing the different types of relation between pinna and the muscles connected with it ; on the left side, extraplatysmal pinna, in the middle supraplatysmal pinna, and on the right side intramuscular pinna.

The attempts to explain the conditions in the echidna must develop into discussion of :

(*a*) Musculo-pinneal relations, such as invasion of pinna by the *panniculus carnosus* in echidna ; or of the acceptance of the above described relations as the primary condition and proceeding to the subsequent separation of pinna by the recession and differentiation of the cutaneous musculature in other mammals.

(*b*) Relating the intramuscular pinna to the way of life of *Tachyglossus*, especially to its defence technique which, at the same time, removes all surface protrusions and develops the powerful musculature for the erection of spines. Lack of sufficient differentiation in cortex, cranial nerves, platysma, and the connections between them cause a basic lack of suitable conditions for facial expression.

The pinna itself is characterized by :

a. The robustness of its cartilage ; *b*. Lack of morphological differentiation of its cartilage and of differentiation into separate cartilages ; *c*. The absence of any structure which can cause friction during the shift due to muscular contraction ; *d*. The fusion of the ventral margins of the cartilage resulting in the formation of the flask-like pinneal cavity ; and *e*. The presence of hair on the internal surface of the pinna.

The robustness of the cartilage and the thickness of its margins are probably related to the strong muscular insertions onto it ; lack of differentiation of separate cartilages may be related to the absence of independent and complicated movements. The absence of morphological differentiation of the cartilage itself is probably a result of the lack of the sound-dispersing function in the ear of echidna.

The smoothness of the median surface of the pinna and its flatness seem, however, to form a more general and therefore a more interesting feature. The median surface of the pinna is smooth in all types of ears, even in the extra- and supra-platysmal ears which can reduce friction by the lateral bending of the pinna. It seems, therefore, that this smoothness of the median surface is phylogenetically a stable morphological feature, independent of the local forces and stresses.

The tubular shape of the pinna stresses again conditions indicated by its embedding in the musculature, and by the presence of hairs, that the external ear in echidna is not involved in the temperature regulative mechanism. The presence of the arterio-venous anastomoses in the echidna ear is nevertheless possible, and needs further investigation.

The most developed specialization in the echidna ear seems to be its protective adaptations ; external hairs and spines guard the external opening of the meatus. All of these—hairs, spines, pinna and meatus—are connected with the cutaneous musculature. The entrance of foreign bodies can be next prevented by the dense hairs on the internal surface of the pinna. The narrowness and angularity of the meatus form another conspicuous protective mechanism : it can protect against the entrance of foreign bodies as well as against high intensity of sound.

In mammals the most common protective device against the high intensity of sound is the increase in the mobility of the pinna so that it can be turned away from the direction of intense sounds. Primates can achieve a similar effect by covering their ears with their hands, but aquatic mammals develop an especially long and angular meatus which serves the same purpose. In echidna, the external acoustic meatus is very long and very angular. It is also essentially an extracranial structure. Because of this extracranial position, passive mobility and frequent changes of plane, the mutual transmission of sound from bone to the meatus is negligible. The intramuscular pinna of the echidna has a poor ability to divert sounds into the meatus. This disability may be partially compensated by the diminishing diameter of each subsequent chamber. In a smaller chamber the same intensity of sound gives a stronger effect or, conversely, a fraction of the number of sound waves passed to a smaller chamber will give the same acoustic effect.

The functional significance of the crista (Plate v, fig. 6) could not be assessed adequately on the material at my disposal.

The external ear of echidna was pictured without description by Westling (1889) and mentioned by Winge (1941). It was also studied in more detail by Ruge (1898) who considered pinna in echidna to be a derivative of the hyoid bone. He found a ramification of the hyoid bone merging with the tympanic cartilaginous ring, which is closely connected with the external acoustic meatus, the latter merging with the pinna. However, the same author found the above connections less pronounced in *Ornithorhynchus*, and intended to prove his point through a series of comparative embryological investigations which, however, to my knowledge were never published. Both the descriptions of Ruge (1898) and Winge (1941) differ from our findings. According to Ruge (1898) the oval pinna is perforated by the canal, and has a transverse process. Winge (1941) did not account for the geniculate structure of the external acoustic meatus. In our material, the pinna was distinctly elongated, no canal or transverse process was observed, and the external acoustic meatus exhibited sharp bendings. The partially cartilaginous and partially membranous structure of the external acoustic meatus in echidna is noted by both previous authors, but not discussed, and its presence was confirmed in the present investigation.

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References

EDGEWORTH, F. H., 1935.—" The Cranial Muscles of Vertebrates ". Cambridge University Press.

McKAY, W. J. S., 1894.—The morphology of the muscles of the shoulder-girdle in Monotremes. PROC. LINN. SOC. N.S.W., 1894, Vol. 9, 2nd Series: 263–360.

RUGE, G., 1898.—Das Knorpelskelet des äusseren Ohres der Monotremen—ein Derivat des Hyoidbogens. *Morph. Jahrbuch*, 25: 202–223. Leipzig.

WESTLING, CHARLOTTE, 1889.—Anatomische Untersuchungen über Echidna. *Bihang till Kong. Svenska Vetensk. Akad. Handl.*, Stockholm, 1889. Afd. IV, Bd. XV, No. 10.

WINGE, H., 1941.—" Interrelations of Mammalian Genera ". Vol. I, 1941. C. A. Reitzels Forlag. Edited by Ad. S. Jensen, D.Sc., R. Spärch, D.Sc., and H. Volsoé, Mag. Sc.

EXPLANATION OF PLATES IV–V

Plate iv

Fig. 1. *Tachyglossus aculeatus*. The topography of the ear. A notch indicates the position of the opening.

Fig. 2. *Tachyglossus aculeatus*. External ear, after removal of the skin.

Fig. 3. *Tachyglossus aculeatus*. The median view of the pinna, in relation to the musculature.

Fig. 4. *Tachyglossus aculeatus*. The resin cast of the external acoustic meatus, showing its bending, and relation to the pinna.

Plate v

Fig. 5. *Tachyglossus aculeatus*. Pinna and external acoustic meatus dissected away from the muscles (lateral view).

Fig. 6. *Tachyglossus aculeatus*. Morphology of the pinna and external acoustic meatus. Pinna completely dissected—note its flatness, close connection with the external acoustic meatus, and the presence of the cartilaginous crista inside the external acoustic meatus.

Fig. 7.—*Tachyglossus aculeatus*. The transverse portion of the external acoustic meatus.

Fig. 8. *Tachyglossus aculeatus*. Entrance of the external acoustic meatus into the skull.